THERMOTROPIC MOVEMENT OF THE LEAVES OF RHODODENDRON MAXIMUM L.

BY JOHN W. HARSHBERGER, PH.D.

It is apparent from a number of recently published papers on the reactions of protoplasm and, in particular, of various sensitive plants to stimuli, that it will be necessary to reconstruct our views to a considerable extent upon the subject of vegetable irritability. The movement of the chlorophyll granules in the cells of leaves, exposed to too bright sunlight; the movement of tendrils in response to shocks, heat or the application of chemical substances, show us that protoplasm reacts in essentially the same manner, whatever plant is chosen for experimentation.

The writer is not aware that any observations have ever been recorded on the movement of the leaves of *Rhododendron maximum*, yet the movements of this plant are quite definite. If observations upon this ericaceous shrub be made during cold weather (the recent zero weather affording fine opportunities for such study), it will be found that the leaves are all bent down closely against the stem, and are rolled inward tightly in a convolute manner, one edge slightly overlapping the other, so that the upper epidermis is alone presented to the action of the weather (fig. 1). To assume this position, the petiole takes a sharp bend downward through an angle of about seventy degrees. The lower side of the petiole is puckered into transverse folds, when the inrolled and hanging position of the leaves is assumed. The acute apex as shown in one of the lower leaves (fig. 1) is slightly incurved. The U-shaped bend of the petiole is more marked in the lower leaves than in the upper. The leaves assume an extremely deep green color, of a brownish hue, and appear as if frozen. Two objects seem to be served by the hanging position of the leaves accompanied by the folding of the lower surface of the blade, which is provided with stomata, or transpiration openings. Firstly, the protection of the lower surface of the leaf, thus ensuring the conservation of the internal water of the plant. When the soil is hard frozen and the days are bright and crisply cold, with a breeze stirring, the plant with broadly expanded leaves would transpire itself to death. Kihlman[1] has clearly shown the action of a dry wind in frosty weather on vegetation to be destructive in the extreme. Secondly, the folding of the leaves and downward curvature facilitates the rapid shedding of snow and ice, which in the mountains where this plant grows cover the evergreen trees and bushes to a considerable extent. During the recent zero weather, even in the most protected places where exposed to the bright sunlight, the drooping condition of the leaves was constantly maintained. In the shade of one of the University buildings, the infolding was even more accentuated than in the sun, as one would naturally expect, and in the mountains of Pennsylvania, in the shadow of the leafless trees and evergreen hemlocks, the cold rigor of the plant was very noticeable at a hundred yards' distance, viewed from the windows of a rapidly moving train.

If a branch of a plant with its leaves in the hanging position be carried into a warm room at about the temperature of 75°–80° F., in response to this thermal stimulus the leaves will begin to unfold and assume the diaheliotropic, or dorsiventral, position. The following observations made upon the reactions to heat and cold stimuli show that the movements are made quite rapidly:

Branch 1.—Intervals of time given in minutes.

1.30 min.—Visible response to heat stimulus.

2.00 min.—Unfolding of leaf began.

3.00 min.—Leaf almost wholly unfolded and petiole erected through an angle of about 40°.

4.00 min.—Upper leaves become dorsiventral.

5.00 min.—Blade of leaves fully expanded, but the petiole not yet entirely straight.

Branch 2.—This branch was held over a radiator. It had been cut for twenty-four hours and placed out of doors in the cold. The record is as follows:

¾–1 min.—Response to stimulus.

1.30 min.—Somewhat jerky upward movement of the petiole apparent.

---

[1] Kihlman, A. O.: Pflanzenbiologische Studien aus Russisch-Lappland, Acta Soc. pro Fauna et Flora fennica (1890).

Schimper, A. F. W.: Pflanzen-geographie auf physiologischer Grundlage (1898), p. 183.

3.00 min.—Leaves assume a nearly horizontal position and the blade unfurled.

4.00 min.—Movement of one of the petioles still evident.

5.00 min.—Leaves assume the normal position.

The main leader showed much quicker response than the laterals. In removing this branch to the cold after it had assumed the normal position in the heated room, it was found that the response under the freezing temperature was not so rapid or marked as when the shoot was moved from out of doors into a heated atmosphere. A slight response to the cold was evident in three minutes, when the petiole began to curve slightly and the blade to roll. At the end of five minutes, the larger leaves were well turned down and rolled. At the end of ten minutes, the large leaves of one of the shoots experimented upon had assumed the cold position.

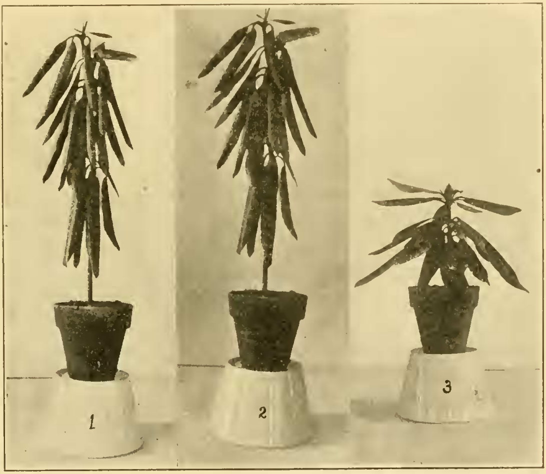

Fig. 1.—Branch in cold rigor position photographed at one-minute interval after being removed to a heated room. The hanging and inrolled position of leaves shown.

Fig. 2.—Branch photographed one minute after the first, showing that the movement of the leaves under the heat stimulus has begun.

Fig. 3.—Branch with fully expanded leaves after a five-minute interval. All of the branches were stuck upright in pots filled with soil, and thus photographed.

Branch 3.—

1 min.—Response to thermal action.

3 min.—Nearly fully expanded.

5 min.—Fully expanded.

Branch 4.—

1 min.—Response to heat stimulus.

2 min.—Snow which had been enclosed by the inrolled leaf dropped out. In fig. 2, the leaves here are yet more fully expanded and the petiole has turned slightly upward, as a critical comparison of figs. 1 and 2 will demonstrate.

4 min.—Leaves nearly fully expanded.

5 min.—Leaves fairly expanded, but the petiole has not responded so quickly, as in the other experimental branches.

Fig. 3 illustrates a branch after it has assumed its normal dorsiventral position.

A cross-section of the leaf shows the following arrangement of cells. There is a thick cuticle developed on the upper surface. Beneath this there are two rows of epidermal cells; the upper row has a thick external wall of cellulose. Beneath the epidermis, there are several well-defined layers of palisade cells, and then follow the loose parenchyma cells, more or less compacted together, succeeded by the lower epidermis provided with stomata and multicellular hairs, so disposed that they form a flat surface of interlocked branches as a protection against too rapid loss of internal water. A striking feature of most of the cells, especially in the upper epidermis, palisade tissue and loose parenchyma tissue, is the intercellular communications, which are visible under ordinary treatment and powers as depressions in the cell-wall. These are of importance as part of the mechanism of movement.

Research has shown that the movement in the leaves of *Mimosa pudica* L., *M. sensitiva* L., *Oxalis bupleurifolia* A. St. Hil., and other sensitives, is brought about by the extrusion of water from the pulvini into the contiguous stems and petioles, resulting in the contraction of the pulvini. When the absorbing tissue of the pulvini have again taken up water, and become tense and firm, they will react again to new stimuli. The study of the cell structure of the leaf of *Rhododendron maximum* L. leads the writer to believe that the transference of liquid from cell to cell, resulting in the alternate rigidity of the upper and lower portions of the petiole, has a very considerable bearing upon the resulting movements. The movements are due to the gradual passage of sap through the contractile protoplasmic sac of each cell into the intercellular spaces, or they in all probability are due to the movement of the liquid from cell to cell by means of the protoplasmic bridges, so that one part of the leaf becomes highly turgescent and the other part more or less flaccid. Cold weather, therefore, sets the liquids in motion toward the upper side of the petiole and leaf. The result of this motion of sap would be the downward flexure of the leaf-stalk and the inward rolling of the leaf. When any branch with hanging leaves is brought into a heated room the liquid is again conveyed to the cells lying near the lower surface and the blade and petiole right themselves. That there is some movement of cell-sap is evident on watching the change of color of the leaves after they are brought indoors. In the cold they are of a blackish green color, but on full expansion they assume a brighter green, which becomes lighter as the temperature of the surrounding air rises.

Turgidity is then the main factor in the mechanism of these movements; its mechanical importance is further strikingly illustrated by the great rigidity of the turgid members, and by the great force, equivalent in parts of some plants to twenty times the atmospheric pressure, which they develop in opposition to external resistance, as when the roots of trees cause the splitting of walls or pavements. Although one essential factor in turgidity is the purely physical osmotic activity of substances in the cell-sap, it must not be forgotten that it also depends upon the resistance offered by the protoplasm to filtration under pressure; so that the maintenance of turgidity is after all a vital act. The maintenance of turgidity appears, in fact, to depend upon a certain state of molecular aggregation of the protoplasm lining the cell-wall, in which it offers resistance to the escape of the cell sap; whereas in the flaccid condition the state of molecular aggregation of the protoplasm is such that it readily permits the escape of cell-sap, under the elastic pressure of the cell-wall, either into the intercellular spaces or through the protoplasmic bridges into adjoining cells, which thus become more turgid.

That evergreen plants, such as *Rhododendron maximum*, have an immense advantage in the struggle for existence goes without saying. The fact that a plant can transpire, can metabolize food, can respire and conduct the elaborated material during the cold of winter is of very considerable biological significance. Other trees and shrubs are practically dormant during the cold of the winter months. They must develop and vegetate during the warmer months of the year, while *Rhododendron maximum* is ready, as our experiments go to prove, to avail itself of all the passing atmospheric and meteorological conditions, whether of winter or summer, which are favorable to its growth.